

TWO NEW OAK HYBRIDS FROM CALIFORNIA

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Quercus × **subconvexa** hybr. nov. (*Q. durata* Jepson × *Q. Garryana* Dougl.) Arbor parva vel arbuscula usque ad 6 m. alta ramulis griseo-brunneis tomentosus demum glabratis vero brunneisque alabastris ovoideis vel sphaeroideo-ovoides hirsutis vel glabratis pallide brunneis 2.5—5 (8) mm. longis foliis denique deciduis in ambitu plerumque obovatis vel latioribus vel ellipticis 4—8.5 cm. longis 2—6 cm. latis paginis superioribus leviter convexis basi cuneatis vel rotundatis haud profunde lobatis vel crasse dentatis dentibus lobisve plerumque mucronatis paginis superioribus aliquanto nitidis eis inferioribus pallidis haud nitidis stellato-pubescentibus petiolis 4—8 mm. longis cupulis hemisphaeroideis 11—16 (-20) mm. latis 6—8 (-11) mm. altis glandibus ellipsoideis 20—22 (-30) mm. longis ca. 12 (usque ad 18) mm. latis.

Small tree to 6 meters in height. Twigs of the current year's growth 1—3 mm. in diameter, from grayish-brown and tomentose when young to glabrate and brown in age, with small, inconspicuous, light-colored lenticels. Buds 2.5-5 (or 8) mm. long, ovoid to round ovoid, hirsute to glabrate, light brown in color. Stipules caducous, 6-7 mm. long, ligulate to spatulate, appressed-pubescent on dorsal surface, light golden-brown. Leaves tardily deciduous, upper surface slightly convex, usually obovate to broadly obovate or elliptical in outline, 4-8.5 cm. long, 2-6 cm. broad, base cuneate or rounded, shallowly lobed or coarsely toothed, the lobes or teeth often abruptly acute with mucronate apices, upper surface somewhat shiny, from stellate pubescent in young leaves to glabrate in age except for sparse, short pubescence along the base of the midrib, lower surface pale and dull, stellate-pubescent; secondary veins 6-8 on a side; petiole 4-8 mm. long, pubescent or glabrate. Staminate catkins to 5 cm. long, rachis puberulent, perianth glabrous except for the ciliate margins of the lobes, stamens glabrous, well-exserted. Acorn cups hemispheric, 11-16 (or 20) mm. broad, 6-8 (or 11) mm. high, base of the scales distinctly tuberculate and covered with fine, light-colored pubescence, the tip flat, broadly triangular to ligulate, pubescent to glabrate and light brown in color, or the tuberculate portion sometimes tapering, keel-like, into the tip; acorn ellipsoid, about 20-22 (or 30) mm. long, about 12 (to 18) mm. broad, glabrate.

Type. Approximately 5 miles north-northeast of Gilroy (Morgan Hill Quadrangle: Section 16, Township 10 S., Range 4 E.); north slope, elev. 1300 feet, Santa Clara County, California, August 27, 1947, *Tucker 1581* (University of California Herbarium No. 938395).

Other collections examined. Type locality: Dec. 15, 1937,

Hendrix 728; May 1, 1946, *Tucker 1393A, B, C, D*; Oct. 5, 1946, *Tucker 1452*; Aug. 27, 1947, *Tucker 1582, 1583, 1584, 1585*; Oct. 7, 1951, *Tucker 2300A, B*. Marin County, California: Three-eighths mile west of Bluff Point, Tiburon Peninsula, Aug. 1, 1947, *Tucker 1576, 1577, 1578*; open serpentine hillside, ca. three-eighths mile east of Tiburon, Aug. 1, 1947, *Tucker 1580A, B, C, D, E, F, G*. Beside Ridgecrest Road, about 7.5 miles southwest of Fairfax, Aug. 31, 1947, *Tucker 1589*; Oct. 7, 1951 *Tucker 2302*.

The fact that oak species belonging to the same subgenus often hybridize when growing in close proximity to one another is well known. No authentic case is known thus far, however, of hybridization between a black oak (subgenus *Erythrobalanus*) and a white oak (subgenus *Lepidobalanus*) under natural conditions, although Pjatnitzky (1946) has reported the experimental production of such hybrids: *Q. borealis* var. *maxima* (of *Erythrobalanus*) \times *Q. Robur* (of *Lepidobalanus*), and *Q. borealis* var. *maxima* \times *Q. macranthera*. In a recent enumeration of interspecific hybrid oaks of North America, Palmer (1948) recognized 80 (a few of them doubtfully), and mentioned that more than 15 others (as yet unnamed) are indicated by specimens in the Arnold Arboretum herbarium and other collections. Eventually the total is certain to be much larger, particularly as the oaks of Mexico and Central America become more thoroughly known. The two hybrids described in this paper are noteworthy because of the remoteness of relationship of the parental species.

The parents of *Quercus* \times *subconvexa* are strikingly different morphologically. *Quercus Garryana* is arborescent (in the part of its range where the hybrid occurs), deciduous, with moderately large, flat, lobed leaves (fig. 1), and occurs most commonly in mesophytic situations in the coast ranges of central and northern California, ranging northward as far as southern British Columbia. *Quercus durata*, on the other hand, is shrubby and evergreen, with small, hard, strongly revolute, toothed leaves. It comprises an element of the chaparral on dry slopes in the coast ranges of California, from Trinity County to Los Angeles County and in the Sierra Nevada foothills of Nevada, Placer and El Dorado counties. It usually occurs on serpentine formations.

This unusual hybrid first attracted the writer's attention when a specimen, *Hendrix 728*, was discovered in a folder of *Q. Garryana* material in the Vegetative Type Map Herbarium in Berkeley. Although it had been identified as *Q. Garryana*, and definitely resembled that species, it seemed obvious, nevertheless, that it was not conspecific.

The possibility of its being a hybrid between *Q. Garryana* and some other white oak was considered. The size of the leaves—in general, smaller than those of *Q. Garryana*—their more shallow lobing, their slightly convex (rather than flat)



Fig. 1. Representative leaves of *Quercus* × *subconvexa*, *Q.* × *Howcllii*, and parental species: A. *Q. durata*, B. *Q.* × *subconvexa* (Tucker 1581), C. *Q. Garryana* (_____), D. *Q.* × *Howelli*, (Tucker 1591), E. *Q. dumosa*.

upper surface, and the fact that they were persisting well into the winter (the collection was made Dec. 15, 1937), suggested an evergreen species with small, non-lobed, strongly convex leaves as the other parent. This combination of characters allowed only one possibility—*Q. durata*. The presence of this species in the same area was confirmed when a sheet was found in the Vegetation Type Map Herbarium with precisely the same collection data as that of the putative hybrid—identical location, date, and collector!

A visit to the collection site revealed the presence of fifty-two small trees, the tallest about fifteen feet in height, forming a small, compact, pure stand only about fifteen yards across. A striking homogeneity in habit and general appearance was immediately apparent throughout the group. It seems probable that the group represents a smaller number of clones. Arising from the soil close in around the bases of many of the trunks, were numerous shoots one foot or less in height. The subterranean portions of several of these shoots were seen to be attached to the main axis (root?) of one tree, about six inches below the soil surface. Some of the fifty-two larger trunks may well have originated in this way from a smaller number of older individuals. Muller (1951) has recently discussed the significance of vegetative reproduction similar to this in various oak species. Indeed, the variety *Breweri* of *Quercus Garryana* typically exhibits this mode of growth.

This stand was near the top of a hill, on a north-facing slope. Immediately below it was a patch of *Q. durata*—low compact shrubs. On this north slope was a mixed growth dominated by *Q. agrifolia* and *Umbellularia californica*, with a scattering of small trees of *Q. lobata*. *Quercus Douglasii* was present on the lower slopes, and a single thirty-foot tree of *Q. Garryana* was found near the foot of the hill, about 250 feet below the location of the putative hybrids.

The evidence seems to justify an assumption of a hybrid origin for these oaks. In addition to the presence of *Q. durata*, and the absence of other shrubby white oaks in their vicinity, they show similarities to *Q. durata* in a number of characteristics: (1) the leaves are slightly convex on the upper side, those of *Q. durata* usually being strongly so, (2) the teeth and lobes of the leaves have mucronate apices, (3) the stellate hairs of upper and lower leaf surfaces respectively are similar in length and relative abundance, (4) minute wart-like protuberances bearing stellate hairs on the upper leaf surfaces, are characteristic of the *Q. durata* at the locality of the hybrids; leaves of the hybrid have similar, but fewer protuberances, (5) the size and shape of the acorns and cups are very similar, and to a lesser degree the cup scales, also, and (6) although this putative hybrid is not shrubby, its small stature could

logically be considered a state intermediate between a larger tree and a shrub, the latter being the habit exhibited by *Q. durata*.

Similarly, morphological evidence strongly indicates *Q. Garryana* as the other parent, although *Q. lobata* and *Q. Douglasii* (all three, of course, being arborescent, deciduous, white oaks) occur in the vicinity, also. *Quercus Douglasii* is eliminated for the following reasons: (1) all herbarium material of this species from Santa Clara County examined, had leaves which, on the average, were smaller and less deeply lobed than those of the hybrid, and (2) the hybrid shows no bluish leaf color (a common feature of *Q. Douglasii*) in either young or mature leaves. Of the other two species, the hybrid is more similar to *Q. Garryana* in all the characters analyzed:

LEAVES. The usually broadly obovate leaf outline in the hybrid, broad, short lobes, and rather shiny upper surfaces all bear a closer resemblance to *Q. Garryana* than to *Q. lobata*.

In the hybrid, the reticulum of veinlets on the upper surface is fine, but conspicuous on close inspection. In this it is similar to *Q. Garryana*; in *Q. lobata* the reticulum is usually quite faint.

STELLATE HAIRS. In length and abundance of stellate hairs on the lower leaf surface, the hybrid resembles *Q. Garryana* much more closely. In *Q. lobata*, these hairs are usually very short and abundant, forming a dense, felt-like covering. In *Q. Garryana*, they are usually distinctly longer, sparser, and almost never form a dense, felt-like indument. In the hybrid these hairs are even longer (varying toward *Q. durata* in this respect) and more sparsely distributed than in *Q. Garryana*.

BUDS. In shape and pubescence of winter buds, the hybrid is closer to *Q. Garryana* than *Q. lobata*. Buds of the former are ovoid to narrow-ovoid, and densely hirsute; those of the latter are round-ovoid and pubescent with fine, mostly closely appressed hairs. Buds of the hybrid are mostly ovoid, from short-hirsute to glabrate.

FLOWERS. The stigmas of the pistillate flowers of the hybrid are spreading and recurved, in this respect similar to *Q. Garryana*. In *Q. lobata*, on the other hand, the stigmas are usually shorter and spreading but not recurved, or only slightly reflexed at the tips.

FRUIT. The fruit of the hybrid shows no suggestion whatever of the large, elongated nut, or deep cup-shaped, strongly tuberculate cup that typify *Q. lobata*. It is, rather, very similar superficially to that of *Q. durata*, although in characters of the cup (notably color and shape of the cup scales) it is intermediate between the *Q. Garryana* and *Q. durata* of the locality.

The hybrid is intermediate between the two parental species not only in morphological characters, but also in the time of flowering and length of leaf persistence.

When first observed by the author, on May 1, 1946, a few of the hybrids were still shedding pollen, but for the most part the staminate catkins were withered and dry. On the shrubs of *Q. durata* at this location new growth was just coming out, and no staminate flowers had started to shed pollen as yet. Although the flowering time of *Q. Garryana* in this locality is not known from direct observation, specimens in the University of California Herbarium show it to be, for California in general, from late March through April (except for var. *Breweri* of higher elevations, which flowers later). Thus, if the latter part of April and the first part of May is the usual flowering period of the hybrids, they are apparently intermediate between the parental species. The occasional occurrence of unusual weather conditions of brief duration tending to retard the flowering of *Q. Garryana* or hasten *Q. durata*, could result in an occasional brief overlap in their flowering periods, thus providing the opportunity for hybridization.

Quercus durata, as mentioned previously, is evergreen, and *Q. Garryana* is deciduous. The hybrid is tardily deciduous, hence intermediate, as indicated by the following observations: *Hendrix 728*, collected December 15, 1937, exhibits numerous green leaves still persisting; on March 30, 1947, the trees of the stand were leafless except for a few persistent dead leaves; and on May 1, 1946, all leaves of the previous season had been shed, all foliage on the trees being new growth.

In March 1947, material was obtained from several members of this stand (*Tucker 1493-1499*), for study of meiosis in pollen mother cells. The haploid chromosome number was found to be twelve. This count agrees with those published by Duffield (1940), Høeg (1929), Jaretzky (1930) and Sax (1930) for other hybrids and species of this genus. No meiotic irregularities were noticed, although a very few tetrads were observed with supernumerary nuclei. These represented 4 per cent or less of the total number of tetrads studied critically. Moreover, an analysis of pollen from specimens taken May 1, 1946, revealed a low percentage (about 3-7 per cent) of abnormal pollen. These observations are similar to those of Sax, who found no more than 8 per cent abnormal pollen in any of the hybrids she investigated, a percentage lying in the same general range (10 per cent or less) exhibited by all but one of the pure species she investigated.

Subsequent to the author's first collections in Santa Clara County, several occurrences of this hybrid in Marin County were brought to his attention by Mr. John Thomas Howell, of the California Academy of Sciences. Howell has since cited them in his "Marin Flora" (1949). The sub-prostrate shrubs on the hillside overlooking the community of Tiburon (*Tucker 1580-A, B, C, D, E, F, G*), cited by Howell, were previously re-

ferred to *Q. Garryana*, by Miss Alice Eastwood (1946). They differ from typical *Q. Garryana*, however, in the following characters, which vary in the direction of *Q. durata*: size and shape of buds; size, lobing, and persistence of leaves, and their somewhat convex upper surface; and the color of persistent, dead leaves. Shrubs of *Q. durata* were noted within 100 yards of this clump, although no *Q. Garryana* was observed in the vicinity. A clump of eight small, shrubby trees, apparently referable to this hybrid, were observed about three-eighths of a mile west of Bluff Point, near the end of Tiburon Peninsula (*Tucker 1576, 1577, 1578*). An individual more obviously intermediate between *Q. Garryana* and *Q. durata* occurs beside Ridgecrest Road, about 7.5 miles southwest of Fairfax (*Tucker 1589, 2302*). At this locality *Q. durata* is abundant but no *Q. Garryana* was observed.

Several attempts have been made to obtain acorns from one or another of the hybrids, to determine whether or not seedlings would show segregation of parental characters. The type locality has been visited three different years with uniformly disappointing results. A single mature acorn represents the largest collection made here so far. The shrubby tree beside Ridgecrest Road, in Marin County, has been slightly more rewarding. The largest collection to date, made on the author's initial visit with Mr. Howell, comprised about a dozen mature acorns. Far more abundant were the numerous abortive acorns which had reached various stages of development. An attempt was made to germinate ten of the mature acorns, but only one rather weak seedling was obtained. Although more data are certainly desirable, the available evidence suggests a high degree of sterility in these hybrids. This would scarcely be surprising in a cross between two such widely dissimilar parents. Whatever the fundamental cause of this apparent inviability of the progeny of *Q. subconvexa*—whether it is due to "cryptic structural hybridity" (Stebbins, 1945, 1950) or to some other cause—the deleterious effect is not clearly revealed until after fertilization. This is indicated by the large numbers of small abortive acorns in all stages of development observed on the Ridgecrest Road hybrid. The high percentage of apparently normal fully-developed tetrads and pollen observed in the original hybrid indicates that no appreciable ill effects have resulted up to the latter stage.

On the trip mentioned above, Mr. Howell also pointed out a group of three small shrubby trees near the top of Fish Grade, between Phoenix and Lagunitas lakes (cited by Howell, 1949, as suspected hybrids between *Q. Garryana* and *Q. dumosa*)? These individuals are described as hybrids as follows:

Quercus × **Howellii** hybr. nov. *Q. dumosa* Nutt. × *Q. Garryana* Dougl.) Arbor parva arbuscula usque ad 5.5 m. alta

ramulis pallide brunneis aliquanto sparse tomentulosis alabastris ovoideis vel sphaeroideo-ovoides puberulentis vel glabratibus pallide rubro-brunneis 3-6 mm. longis foliis (an denique?) deciduis in ambitu ellipticis vel obovatis 4-10 cm. longis 2-6 cm. latis basi cuneatis attenuatis vel rotundatis plerumque inaequalibus margine inaequaliter ac haud profunde lobatis vel dentibus vel lobis plerumque mucronatis crasse dentatis paginis superioribus nitidis atroviridibus eis inferioribus pallide veridibus hic haud nitidis pilis brevissimis puberulentis cupulis valde vel leviter patelliformibus 14-18 mm. latis 5-8 (plerumque 6) mm. profundis glandibus ovoideis vel ellipsoideis 20-30 mm. longis 13-19 mm. latis.

Small tree to 5.5 meters in height. Twigs of the current year's growth 1.5-3 mm. in diameter, light brown and rather sparsely tomentulose with small, light-colored lenticels. Buds 3-6 mm. long, ovoid to round-ovoid, puberulent and with the margins of the scales ciliate, to glabrate, light reddish-brown in color. Stipules mostly caducous, to 8 mm. long, oblong to linear, sparsely puberulent on dorsal surface, light brown in color. Leaves deciduous (tardily?), elliptical to obovate in outline, 4-10 cm. long, 2-6 cm. broad, base cuneate, attenuate, or rounded, often unequal, irregularly shallowly lobed or coarsely toothed, the apices of teeth or lobes usually mucronate, upper surface dark green and shiny, sparsely stellate-puberulent to glabrate, lower surface light green and dull, very short-puberulent; secondary veins mostly 6-8 on a side; petiole 3-10 mm. long, puberulent. Staminate catkins not seen. Acorn cups saucer-shaped to shallow cup-shaped, 14-18 mm. broad, 5-8 (mostly about 6) mm. high, scales narrowly ovate or lanceolate, minutely puberulent, bases of the scales with pronounced but small tubercles, the tips sometimes more or less ligulate; acorn ovoid to ellipsoid, 20-30 mm. long, and 13-19 mm. broad, brown and glabrate.

Type. Near top of Fish Grade, between Phoenix Lake and Lake Lagunitas, Marin County, California, August 31, 1947, *Tucker 1591* (University of California Herbarium no. 938397).

Other collections examined. Type locality: August 31, 1947, *Tucker 1592, 1593*.

These shrubby trees resembled *Q. Garryana* in having rather large leaves with dark green, shiny upper surfaces, and one which bore fruit had shallow, saucer-shaped acorn cups closely resembling those of the latter species. They were obviously not conspecific, however; the leaves were, in general, smaller than in *Q. Garryana*, and coarsely toothed, or at most shallowly lobed. Moreover, the lobes or teeth had distinctly mucronate apices.

As in the preceding case, it seemed likely that these individuals were hybrids between *Q. Garryana* and a shrubby, evergreen, white oak with small, mucronately toothed leaves.

In this case the few shrubby oaks in the vicinity were not *Q. durata*, but *Q. dumosa*, and in several morphological characters these trees resemble the latter rather than the former:

1. The leaves are not convex above, but plane.
2. The stellate hairs of the lower leaf surfaces are quite short—definitely shorter than those of either *Q. durata* or *Q. Garryana*.
3. The branchlets of the current year's growth are sparsely to moderately puberulent with very short hairs.
4. The buds, in shape and color, are quite similar to those of *Q. dumosa*, but are considerably larger, approaching the size of those of *Q. Garryana*.

Staminate flower buds were collected March 8, 1953 for study of meiosis. The haploid chromosome number was found to be twelve.

The largest of these three individuals—a small, shrubby tree about 18-20 feet tall—bore a few mature (or nearly mature) acorns, although no abortive ones were observed on the tree. An attempt was made to germinate 18 of these, but no seedlings were obtained. It may well be that this hybrid is highly sterile, as seems to be the case in *Quercus* × *subconvexa*. As in the latter this would not be surprising, for *Q. dumosa* is scarcely, if at all, any more closely related to *Q. Garryana* than is *Q. durata*.

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